
Tropidogyne, a New Genus of Early Cretaceous Eudicots (Angiospermae) from Burmese Amber

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ABSTRACT. †*Tropidogyne pikei* K. L. Chambers, Poinar & R. T. Buckley, representing a new genus and species, is described from an Early Cretaceous flower preserved in Burmese amber. †*Tropidogyne* may occupy a stem or early crown position in the phylogeny of the rosoid clade. Its floral morphology, while largely plesiomorphic, can be compared with the modern family Cunoniaceae. The flower of the fossil taxon is small, bisexual, epigynous, apetalous, with five regular sepals slightly connate at the base, 10 stamens, the one preserved anther having two thecae that dehisce by longitudinal slits, an ovary of three carpels surmounted by a conspicuous disc, three short, acute styles, and a 10-ribbed inferior ovary. At the summit of each rib of the †*Tropidogyne* ovary is a small, darkly stained patch of tissue, interpreted here as a secretory gland.

Key words: Amber, Burma (Myanmar), Cunoniaceae, Early Cretaceous, eudicot flower, eurosoid clade, fossilized resin.

Burmese amber has yielded a wealth of arthropod and plant remains (Poinar et al., 2005), including some very interesting angiosperm fossils. These include flowers with affinities to the family Monimiaceae (Poinar & Chambers, 2005), Cornaceae (Poinar et al., 2007b), and the rosoid clade of eudicots (Poinar et al., 2008), as well as two early bambusoid grasses (Poinar, 2004). In the present paper, we describe an additional flower from the same amber deposit in the Hukawng Valley in Burma (Myanmar).

MATERIALS AND METHODS

The amber was derived from a mine first excavated in 2001, in the Hukawng Valley, southwest of Maingkhwan in the state of Kachin (26°20'N, 96°36'E) in Burma (Myanmar). This new amber site,

known as the Noiye Bum 2001 Summit Site, was assigned to the Upper Albian of the Early Cretaceous on the basis of paleontological evidence (Cruickshank & Ko, 2003), placing the age at 97 to 110 million years ago (Ma). Nuclear magnetic resonance (NMR) spectra and the presence of araucaroid wood fibers in amber samples from the Noiye Bum 2001 Summit site indicate an araucarian (possibly *Agathis* Salisb.) tree source for the amber (Poinar et al., 2007b).

The well-preserved flower (accession #ab 14), with two missing sepals, is in a rectangular piece of amber 11 mm long, 6 mm wide, and 3 mm thick. Examination and photographs were made with a Nikon stereoscopic microscope SMZ-10 R (Nippon Kogaku K. K., Tokyo, Japan) at 80× and a Nikon Optiphot microscope (Nippon Kogaku K. K.) at 800×. The specimen is deposited in the R. T. Buckley amber collection, Florence, Kentucky 41042-8355, U.S.A., and can be examined by contacting Mr. Buckley, phone (859) 384-8649.

†***Tropidogyne*** K. L. Chambers, Poinar & R. T. Buckley, gen. nov. TYPE: †*Tropidogyne pikei* K. L. Chambers, Poinar & R. T. Buckley.

Genus fossile a *Ceratopetalum* Sm. flore tricarpellato (nec bicarpellato), ovario infero (nec semiinfero) atque disco non pubescenti, a †*Platydisco* Schönerberger & Friis flore tricarpellato (nec tetracarpellato) apetalum (nec tetrapetalum) atque ovario infero (nec semiinfero) differt.

Flowers small, bisexual, actinomorphic, epigynous, glabrous; petals none; sepals 5, regular, slightly connate at base, ovate-lanceolate, explanate, with midvein and 3 to 5 minor veins from the base, veins conspicuously anastomosing above; epigynous disc darkly pigmented, 3-lobed, with an irregular margin; stamens 10, diplostemonous, filaments slender, at-

tached at outer edge of disc; anthers basifixed or dorsifixed, with 2 thecae dehiscing introrsely(?) by longitudinal slits, connective not prolonged; gynoecium 3-carpellate, ovary inferior, styles 3, short, arched-divergent, arising separately from disk, tips acute, stigmas not defined; exterior surface of ovary with 10 pronounced longitudinal ridges, each ridge with a distal pad of differentiated, perhaps glandular, tissue.

Etymology. The generic name is taken from the Greek “tropis,” for “ridge” or “keel,” and “gyne,” for “woman” or “pistil,” referring to the distinct ridges on the inferior ovary.

†*Tropidogyne pikei* K. L. Chambers, Poinar & R. T. Buckley, sp. nov. TYPE: Burma (Myanmar). Kachin: amber mine in the Hukawng Valley SW of Maingkhwan, 26°20'N, 96°36'E, T. Pike #ab 14 (holotype, Burmese amber, R. T. Buckley collection, Florence, KY). Figures 1–3.

Flower ca. 5.1 mm diam.; sepals 1.89–1.97 × ca. 1.05 mm; stamens 10, most filaments damaged and anthers missing, only one complete stamen with anther present; filament ca. 0.76 mm; anther ca. 0.16 × 0.24 mm; filaments of remaining stamens (all without attached anthers) ranging in length from 0.08 to 0.58 mm; ovary inferior, ca. 1.30 mm; remaining peduncle ca. 1.1 mm.

Etymology. The specific epithet honors the discoverer of the flower, Ted Pike.

DISCUSSION

Concerning the preservation of the fossil, the lower two sepals are broken off by a fracture in the amber (they are reconstructed in Fig. 2), and this allows close examination of the inferior ovary from the side. The face of the flower is well spread for viewing (Figs. 1A, 3). Although most of the stamens are broken, one stamen retains its anther (Fig. 1A, left insert), showing that the flower was bisexual in organization. The disc is conspicuous, darkly stained, and bears three short, curved, acute styles. The disc has an irregular margin and is trilobed (Fig. 3A), each lobe assumed to correspond to a carpel. If the disc was secretory, the dark coloration may be an artifact from chemical alteration of nectar on its surface. The reticulate venation of the sepals, with several veins entering from the base, is particularly evident (Fig. 3B), as is a slight connation of sepal tissue near the base. The anthers dehisce on one side by two longitudinal slits (Fig. 1A, left insert), and we suggest that this dehiscence was introrse based on the similarity to certain anthers of Cunoniaceae, as

discussed below. Insertion of the filament, which appears basal, would instead be dorsal by similar analogy to these comparable anthers. A notable feature of the ovary is that it has 10 prominent longitudinal ridges or ribs, with five ribs opposite the sepals and five alternating with the sepals (Fig. 1B). On one side of the ovary we noted that each rib has a dark-staining triangular pad of tissue at its distal end (Fig. 1C). This is a regular feature, not an artifact, on all the ribs in this field of view. In other views, this dark tissue appears to be frayed or macerated. We interpret this tissue to be a specialized gland, perhaps secretory, found regularly on all the ribs of the ovary immediately outside the base of the calyx.

For purpose of discussion of an ancient fossil like †*Tropidogyne*, it is useful to present a hypothesis concerning a possible systematic assignment, which may lie with the eurosid clade of eudicots. The type specimen is dated as Late Albian, a time period during which the rosid clade underwent its principal ordinal diversification (Magallón & Castillo, 2009: 352, fig. 1). The genus may represent a stem group or an early member of one of the crown clades. Its floral morphology does not present any obvious apomorphies. Apetaly occurs in at least 10 modern families of rosids (Endress & Matthews, 2006: 231, fig. 11), and it is uncertain whether or not this feature is plesiomorphic in the entire clade. The presence of ribs on inferior ovaries is also common in extant flowers. Their number is often twice the number of sepals because they are formed over the vascular traces (median and synlateral) of the sepals (Endress, 2008: fig. 13). In several salient features, the floral morphology of †*Tropidogyne* resembles members of Cunoniaceae, tribe Schizomerieae, in particular the genus *Ceratopetalum* Sm. Our discussion is based on the descriptions, anatomical studies, and excellent SEM illustrations of this genus from the works of Engler (1930), Hoogland (1960), Dickison (1975, 1989), Hufford and Dickison (1992), Matthews et al. (2001), Bradford and Barnes (2001), Hopkins and Hoogland (2002), Rozefelds and Barnes (2002), Matthews and Endress (2002), and Bradford et al. (2004).

In general form, the fossil resembles *Ceratopetalum* in its regular, spreading calyx of five lanceolate-ovate sepals. The similarity in sepal venation is especially pronounced when comparison is made with modern *Ceratopetalum* (Barnes & Hill, 1999: 638, figs. 3–6) and with the Late Eocene–Early Oligocene fossil †*C. wilkinsonii* R. W. Barnes & R. S. Hill from Australia (Barnes & Hill, 1999: 639, fig. 11; Rozefelds & Barnes, 2002: 670, fig. 10C). Due to obscuring pigmentation, it is not possible to tell whether there is basal fusion of the lateral veins of adjacent sepals in

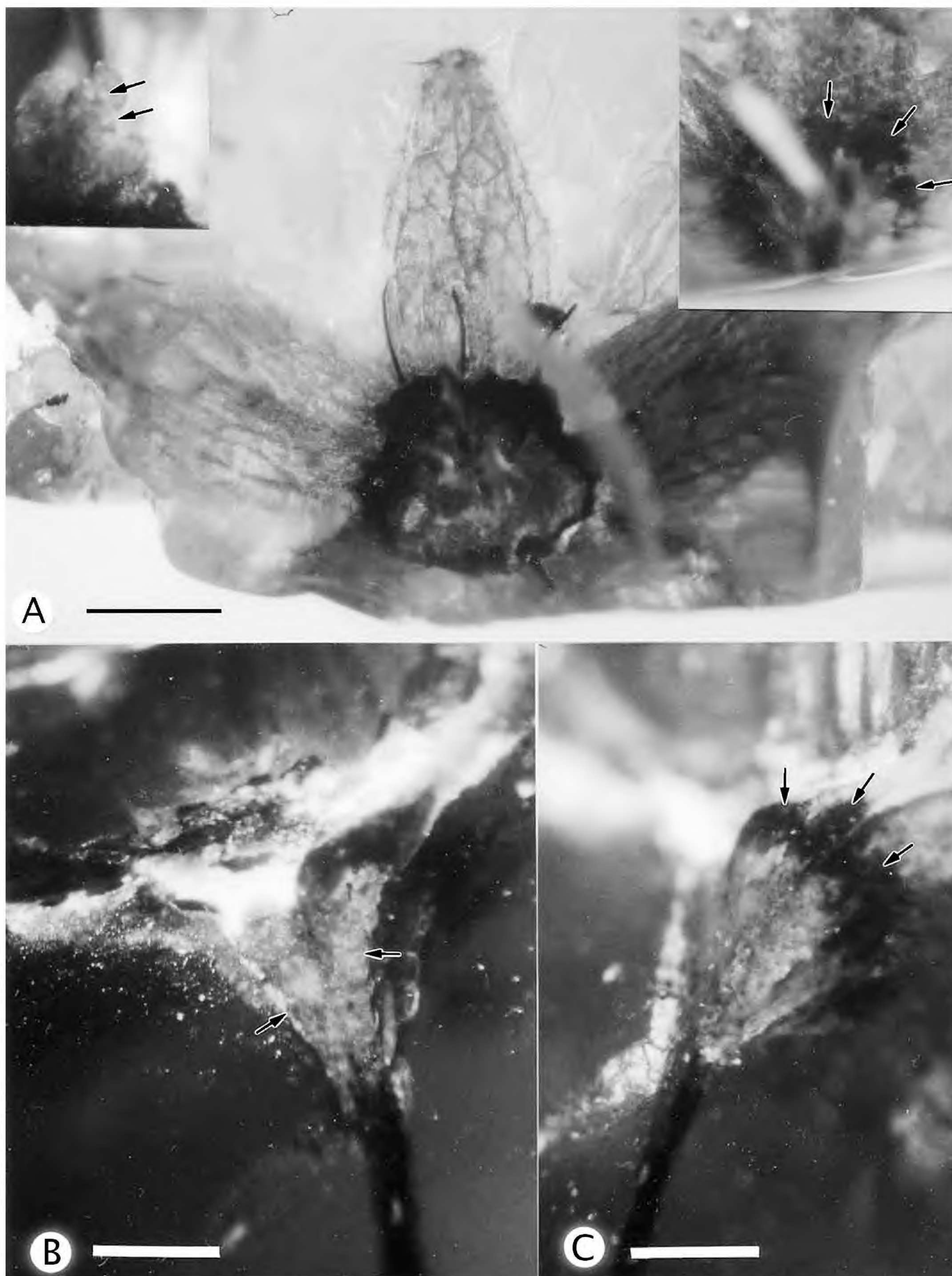


Figure 1. Flower of *Tropidogyne pikei* in Burmese amber. —A. Holotype, T. Pike #ab 14. Right insert shows base of flower (arrows show darkened tissue); left insert shows single remaining anther with pollen (arrows) resting on the dehiscent valves. —B. Exterior of ovary showing ridges (arrows). —C. View of darkened tissue (arrows) at distal end of ridges on ovary. Scale bars: A = 0.71 mm; B, C = 0.55 mm.

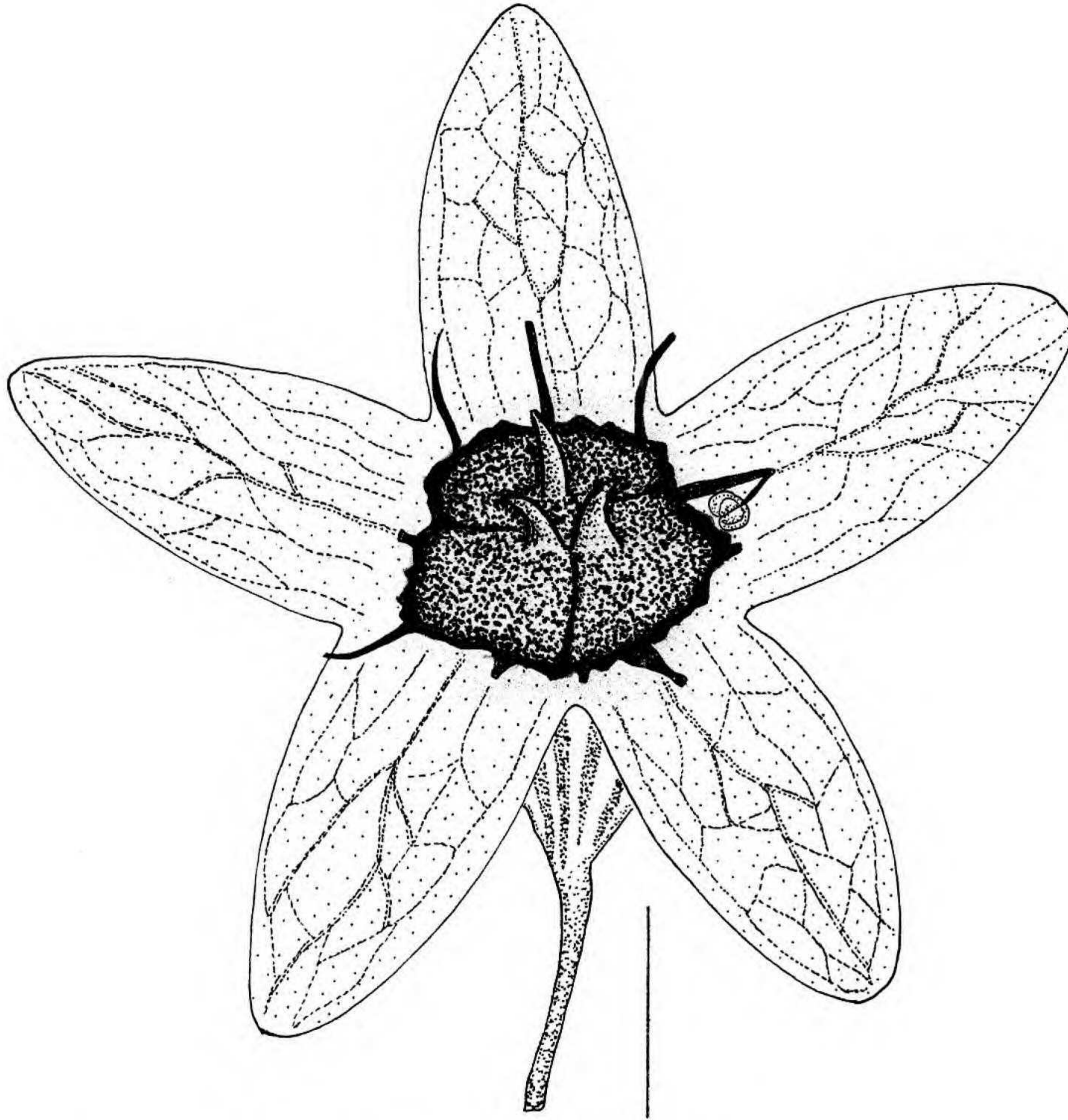


Figure 2. Partial reconstruction of *Tropidogyne pikei*. Scale bar = 1 mm.

†*Tropidogyne*, as described for *C. gummiferum* Sm. (Barnes & Hill, 1999). *Ceratopetalum* sepals are persistent, enlarged, leathery, and assist in dispersal of the dry indehiscent fruits (pseudosamaras, cf. Hopkins & Hoogland, 2002: 76), hence they are well preserved as fossils. †*Tropidogyne* is apetalous, as are eight of the nine species of *Ceratopetalum* (Rozefelds & Barnes, 2002). *Ceratopetalum gummiferum* has five wedge-shaped, 3-toothed petals (Engler, 1930; Matthews et al., 2001: 445, fig. 8). The related genus *Schizomeria* D. Don (Cunoniaceae) differs from the above two genera in being hypogynous (Bradford & Barnes, 2001).

The androecium of both †*Tropidogyne* and *Ceratopetalum* is diplostemonous, with subulate filaments and small, bithecal anthers (Dickison, 1989: 55, fig. 4.2 F; Rozefelds & Barnes, 2002: 658, fig. 5). The remaining anther of the fossil described herein (Fig. 1A, left insert) shows unifacial dehiscence by slits, which very much resembles the introrse anthers of, e.g., *C. tetrapterum* Mattf. (Rozefelds & Barnes, 2002: 659, fig. 6J and other anthers there illustrated). Our interpretation of introrse dehiscence for the fossil is based on this similarity to the modern genus.

The gynoecium of *Ceratopetalum* is consistently bicarpellate (Hopkins & Hoogland, 2002; Bradford et al., 2004), but the tricarpellate condition of †*Tropid-*

ogyne is found as a variation in *Schizomeria* (Hopkins & Hoogland, 2002) as well as elsewhere in Cunoniaceae (Bradford et al., 2004). In both †*Tropidogyne* and *Ceratopetalum* the styles arise separately from a conspicuous epigynous disc and are similar in being short, curved-divergent, and acute (Rozefelds & Barnes, 2002: 658, fig. 5). In both, the stigmas are scarcely defined; Matthews et al. (2001: 448, fig. 34) illustrate the stigma of *C. gummiferum* as a papillate region at the very tip of the style. The ovary of *Ceratopetalum* is described as half-inferior (Hoogland, 1960; Dickison, 1975: 441, fig. 21; Bradford & Barnes, 2001; Bradford et al., 2004), but this is developmentally variable in the genus. For example, in the serial cross sections illustrated by Matthews et al. (2001: 442, fig. 4) for a flower bud of *C. gummiferum*, the locules and ovules in the ovary are located below the level of attachment of the sepals to the receptacle, whereas in developing fruits, the ovary comes to be one half or more superior (Chambers, pers. obs.). The ovary of †*Tropidogyne* appears to be entirely inferior, although we were not able to observe the location of locules and ovules. The ridges on the ovary of †*Tropidogyne* are matched in *C. gummiferum* by 10 projecting ribs forming pronounced ridges on the ovary of flowers and developing fruits (Chambers, pers. obs.). This species otherwise differs from

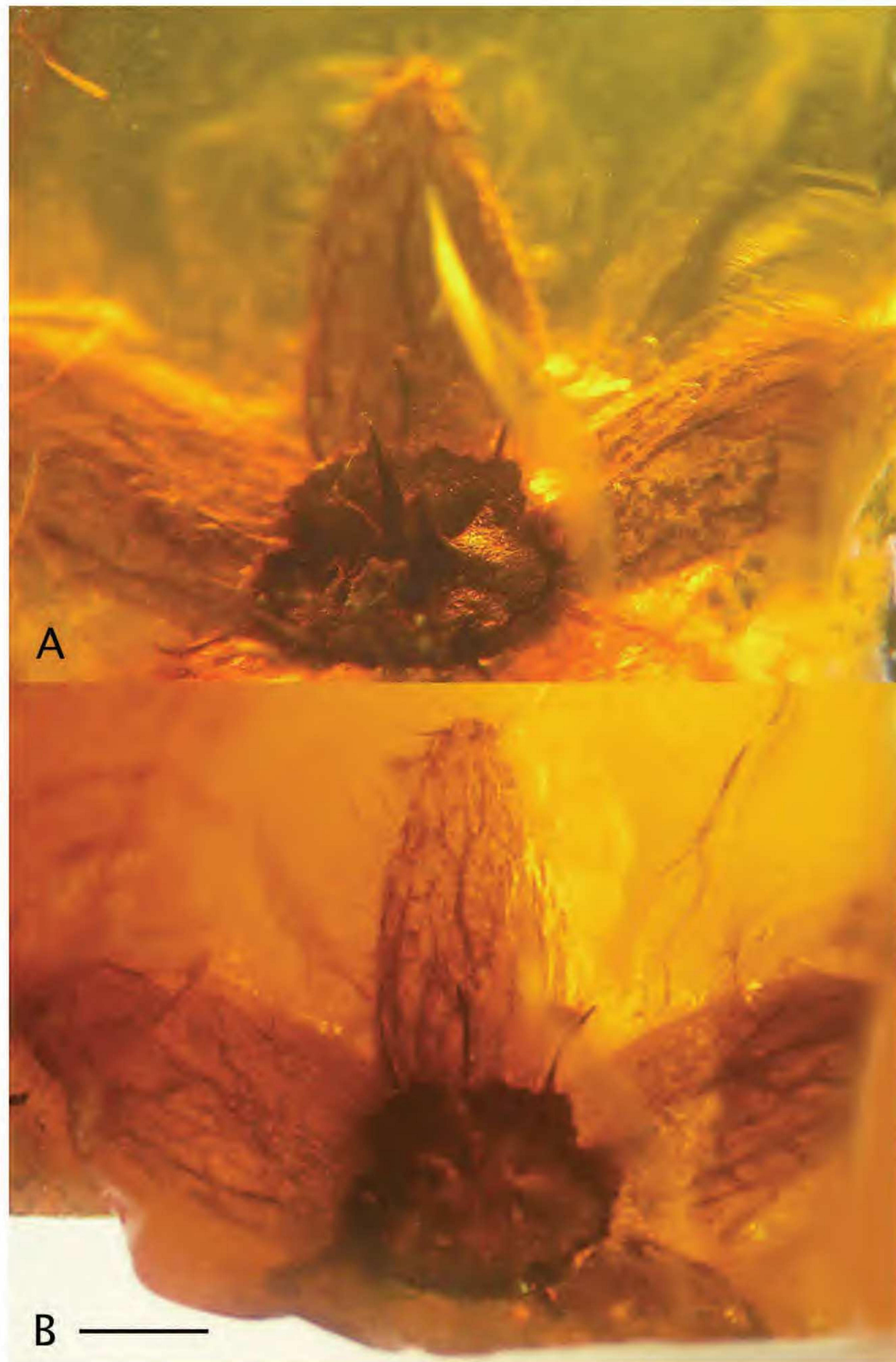


Figure 3. Holotype specimen of *Tropidogyne pikei*. —A. Focal plane showing epigynous disk and styles (photo by R. T. Buckley). —B. Focal plane emphasizing sepal venation (photo by G. O. Poinar). Scale bar = 0.64 mm.

†*Tropidogyne* in having fimbriate petals and a bicarpellate pistil.

The slight basal connation of the sepals of †*Tropidogyne* is not present in *Ceratopetalum*. Further, as best we can determine, the anther of †*Tropidogyne* does not have a prolongation of the thecal connective, as is common in genera of tribe Schizomerieae (Bradford & Barnes, 2001; Rozefelds & Barnes, 2002: 659, fig. 6). However, in some *Ceratopetalum* species the projection can be very small (Rozefelds & Barnes, 2002). Differences are also evident between †*Tropidogyne* and *Ceratopetalum* with respect to the epigynous disc. In the former, the disc is segmented into three lobes representing the three carpels (Fig. 3A), and there is no circumferential ring of swollen tissue as in *Ceratopetalum* (see SEM illustrations in Dickison, 1989: 55, fig. 4 F; Rozefelds & Barnes, 2002: 658, fig. 5). The disc of †*Tropidogyne* is not pubescent

around the base of the styles, whereas this is a common feature in *Ceratopetalum*. These various differences between the fossil and the modern genus suggest that the similarities are due to plesiomorphic traits that may not imply a direct phylogenetic link.

The regular occurrence of a gland, or of macerated dark-stained tissue, on each ridge is an evident feature of †*Tropidogyne*. Because of the uncertain nature of these structures, we are not hypothesizing a possible function of such glands.

The charcoalfied flower †*Platydiscus peltatus* Schönenberger & Friis, from the Late Cretaceous, has been compared with Cunoniaceae or the structurally similar Anisophylleaceae (Schönenberger et al., 2001). This fossil has been dated to Late Santonian–Early Campanian (80+ Ma). In reconstructions (Friis et al., 2006; Schönenberger & von Balthazar, 2006), it shares features with both †*Tropidogyne* and *Ceratopetalum*

but is 4-merous, tetracarpellate, and petaliferous. There is an annular, lobed disc from which the eight stamens arise, and the ovary is half-inferior. The short, acute, recurved styles (as reconstructed) are reminiscent of †*Tropidogyne* and *Ceratopetalum*. The floral similarities of †*Platydiscus*, *Anisophyllea* R. Br. ex Sabine, and Cunoniaceae, including *Ceratopetalum*, were described by Matthews et al. (2001), who concluded that further study is justified concerning the phylogenetic position of Anisophylleaceae (Cucurbitales, based on *rbcL* phylogeny as noted by Stevens, 2001 on; APG II, 2003). These authors (Matthews et al., 2001; see also Schönenberger & von Balthazar, 2006) question whether the many floral similarities of Anisophylleaceae to Cunoniaceae represent convergent evolution in the Oxalidales and Cucurbitales, or a suite of plesiomorphic features of rosids established in the Late Cretaceous and retained in the two families. We would point out that †*Tropidogyne*, with its similarity to *Ceratopetalum* as well as to †*Platydiscus*, moves the origin of this floral syndrome back to the Early Cretaceous with a probable age of at least 100 Ma.

A review of earlier estimates of the ages of crown and stem groups of basal eudicots (Wilkström et al., 2001; Crepet et al., 2004; Anderson et al., 2005) was provided by Magallón and Castillo (2009). In their analysis, a rapid diversification of eurosid lineages in the last five million years of the Albian was inferred, using molecular methods and known fossil reference points (see also Friis et al., 2006). The present report and other examples of flowers that have recently been described from Burmese amber of the Late Albian (Poinar, 2004; Poinar & Chambers, 2005; Poinar et al., 2007a, 2008) help to document this important segment of eudicot evolution.

†*Tropidogyne* may have been insect-pollinated, as proposed earlier by Santiago-Blay et al. (2005), perhaps being visited by †*Melittosphex burmensis* Poinar & Danforth, a small bee described from the same amber deposits (Poinar & Danforth, 2006).

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